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New record for Colombia, updated distribution map, and comments on the defensive behavior of *Thamnodynastes dixoni* Bailey & Thomas, 2007 (Serpentes, Dipsadidae, Xenodontinae)

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Abstract

The original description of *Thamnodynastes dixoni* Bailey & Thomas, 2007 was based on few specimens, and the morphological variation, distributional range, and ecological aspects of this species are virtually unknown. The species is known to occur in the Llanos of Colombia and Venezuela. In Colombia, it was recorded only in four localities. We report a fifth occurrence of *T. dixoni* in Colombia and the first in the Department of Meta. The new record extends this species' distribution nearly 150 km (in a straight line) from the nearest previously known occurrence at Paz de Ariporo, Department of Casanare. Additionally, we also provide comments about the species' defensive behavior, not reported elsewhere, and a thorough revision on the species' geographical distribution.

Keywords

Apure-Villavicencio dry forest, La Costa Xeric shrublands, Llanos, natural history, range extension, South America, Tachymenini.

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Introduction

The snake genus *Thamnodynastes* (Dipsadidae, Xenodontinae, Tachymenini) represents a South American lineage that comprise 20 nominal species which are widely distributed in a vast array of forested and open landscapes from Colombia and Venezuela south to northern Argentina (Bailey et al. 2005; Bailey and Thomas 2007; Coelho et al. 2013; Franco et al. 2017; Guedes et al. 2018). The genus has its greatest diversity in Brazil, with 12 species (Costa and Bérnils 2018), while only four species are recorded in Colombia: *Thamnodynastes dixoni* Bailey & Thomas 2007, *T. gambotensis* Pérez-Santos & Moreno 1989, *T. pallidus* (Linnaeus, 1758), and *T. paraguanae* Bailey & Thomas, 2007. *Thamnodynastes dixoni* is a cis-Andean species inhabiting the Llanos of Venezuela and Colombia (Bailey and Thomas 2007; Rivas et al. 2012; Natera et al. 2015). This species is known to occur

in gallery forests, shrub lands, and flooded savannahs (Angarita-Sierra 2014; Pedroza-Banda et al. 2014; Natera et al. 2015). In Colombia, it has been recorded since its description in four localities, which are in the departments of Arauca (Cravo Norte River near the border between Colombia and Venezuela; Bailey and Thomas 2007), and Casanare (ca. 168 km southwest of Arauca) (Angarita-Sierra 2014; Pedroza-Banda et al. 2014; Trujillo 2015; Mora-Fernández 2016). However, information on the natural history and distribution of this species remains poorly known.

The Llanos (Lasso et al. 2010; Dinnerstein et al. 2017) is a vast Neotropical natural area (over 1 million square kilometers) found in central-western Venezuela and eastern Colombia. It is characterized by a continuous matrix of tropical grasslands in conjunction with gallery forests and flooded areas, associated with a hydrographic web composed of rivers, ponds, and even periodically flooded grasslands and forests (Lasso et al. 2010). The region is also characterized by rainfall seasonality, oligotrophic soils, and frequent fires (Sarmiento 1984). Recently, Dinnerstein et al. (2017) proposed an ecoregion-based approach to protect biomes of the world and split the Llanos into three ecoregions: Orinoco savannahs, Apure-Villavicencio dry forest, and La Costa Xeric shrub lands. In Colombia, the Llanos has low species richness and endemicity for amphibians and reptiles compared to other natural ecoregions, such as Andean forests and Amazonia (Lynch et al. 1997, 2016; Acosta-Galvis 2000; Acosta-Galvis et al. 2010; Lynch et al. 2016). Snakes represent an interesting and poorly known clade of vertebrates, which constitutes a good model to evaluate biogeographical patterns (Guedes et al. 2014; 2018). However, despite recent advances and an increase in fieldwork in some areas, there is still a lack of distribution data for a considerable number of snake species in the Neotropics, including species of the Llanos in northern South America.

To assist in filling gaps in the distribution of snake species in Colombia, we provide an updated database of the distributional records of *T. dixoni*, a poorly known species, and provide the southernmost record of the species in the country. We also present an updated map of the known geographic distribution of *T. dixoni*, which includes both the new record and data from the literature. Additionally, we also report on the defensive behavior of a recently collected specimen.

Methods

During fieldwork by one of us (JARM) as part of an environmental license for oil exploration, a specimen of *T. dixoni* was found alive in a forested area of the municipality of Puerto Gaitán, Department of Meta, Colombia. The specimen was collected under permit no. 1166 (Resolution 1166 from 9 October 2014) granted by the National Authority for Environmental Licensing (ANLA) to the University of Caldas. It was euthanized using 2% Xylocaine, fixed in 10% formalin, and kept preserved in 70% ethanol. A tissue sample for DNA was taken. The specimen was deposited at the herpetological collection of the Museo de Historia Natural Universidad de Caldas (MHN-UCa), Manizales, Colombia. We measured snout–vent length (SVL) and tail length (TL) in millimeters using a tape measure. Ventral and subcaudal scales were counted following Dowling (1951).

We performed a literature review of the occurrences of *T. dixoni*, including only those records having vouchered specimens and containing morphological data (mostly from taxonomic studies). We prepared an updated distribution map (Fig. 1) for the species using QGIS 2.14 (QGis Development Team 2018). The description of defensive behaviors follows terminology by Greene (1988).

Results

***Thamnodynastes dixoni* Bailey & Thomas, 2007**
Figures 1–4

New record. COLOMBIA • 1 ♂ adult (MHN-UCa 0257), 380 mm SVL, 132 mm TL, 34% proportion tail length/total length; Department of Meta, Municipality of Puerto Gaitán, Nuevas Fundaciones village; 04.215034°S, 072.054604°W; 177 m a.s.l. (Table 1, Fig 1); 6 Oct. 2014; collected by Julián A. Rojas; found at 19:45 h active hanging on a shrub at 120 cm from the ground, within a flooded gallery forest dominated by "Palma de Moriche", *Mauritia flexuosa* (Arecaceae).

Identification. The specimen (MHN-UCa 0257, Fig. 3) was identified following Bailey and Thomas (2007) and was verified by Luis F. Esqueda based on the following diagnostic characters: dorsal scale row 19-19-15, weakly keeled above the third row, two preventrals, 149 ventrals, cloacal plate divided, 74 subcaudals, eight supralabials with fourth and fifth entering the orbit, nine infralabials with the first five contacting the two pair of shin shields, frontal single, paired internasals, paired prefrontals, one supraocular, two preoculars, two postoculars, two anterior temporals, three posterior temporals, elliptical pupils, opisthoglyphous dentition with 10+1 maxillary teeth. Dorsal background color is copper-light brown, with a general blotched pattern of brownish, blackish, and whitish squares, sparsely delineated along the body on longitudinal sense (Figs 2A, 3). The posterior part of the body is copper colored from the fourth dorsal scale to the paravertebral region. First four dorsal scales are brown with a black delineated line across the top of fourth scale row. Ventrally, it is cream colored with four brown longitudinal lines, and the two outer lines bordering the outer limit of the ventral scales are more conspicuous. This ventral pattern of lines is accentuated from the ventral scale 26 to the cloacal plate. From the beginning of the tail and as far as the 39 subcaudal scale, only three longitudinal lines are visible (Figs 2, 3).

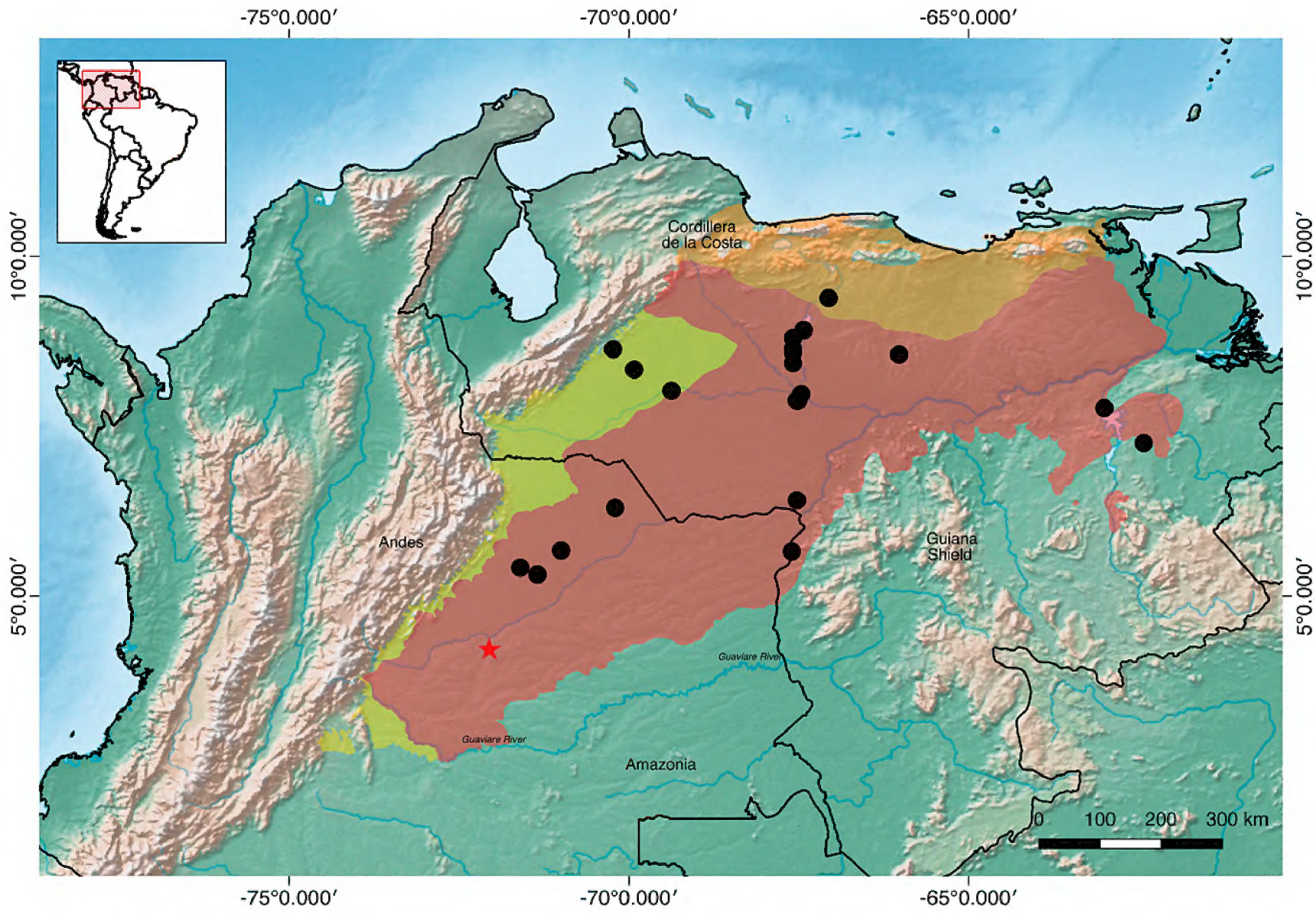

Figure 1. Distribution of *Thamnodynastes dixoni* including the new record. Black circles: published records; Red star: new record in the Nueva Fundaciones village, Municipality of Puerto Gaitán, Department of Meta, Colombia. Ecoregions classified according to Dinerstein et al. 2017 (avaliable at https://ecoregions2017.appspot.com): brown area shows the boundaries of the Llanos, yellow-green area shows the limits of Apure-Villavicencio dry forest, and orange area is the limits of the La Costa xeric shrublands.

Figure 2. *Thamnodynastes dixoni* (MHN-UCa 0257). **A.** found active at 19:45 h, 120 cm above the ground. **B.** Flooded gallery forest of the Llanos ecoregion in Puerto Gaitán, Meta, Colombia. Photographs by JARM.

Defensive behavior. When the individual was captured and handled, it showed no defensive behavior or attack attempt. However, while photographs were being taken (during the morning after capture in captive conditions), the snake became more active and displayed different behaviors. At first it expanded the head laterally to simulate a triangular shape (Fig. 4A), but after JARM touched its body with a pencil, the snake flattened the first half of the anterior portion of its body in an S-coil shape, with the head laterally enlarged (Fig. 4B). Finally, when the pencil was moved laterally at a 30–40 cm distance from the snake, it raised and stroked several times, gaping its mouth. While manipulating this individual, it did not eject any cloacal discharge.

Discussion

This is the first published vouchered record of *Thamnodynastes dixoni* for the department of Meta, Colombia. This new record at Nuevas Fundaciones village extends the known distribution of this species 151 km southwest from previously known occurrences in the Department of Casanare and and 310 km southwest from Cravo Norte River in Department of Arauca. The new record increases Extent of Occurrence (EOO) of *T. dixoni* from 21,983,634 km^2 to 24,297,212 km^2. Biogeographically, the new record is the southernmost for *T. dixoni* in the flooded savannas of the Llanos. Other species of reptiles, such as *Bothrops atrox* (Linnaeus

Table 1. Literature and herpetological collection data of occurrences of *Thamnodynastes dixoni* in Venezuela and Colombia. Source of records: 1 = Bailey and Thomas (2007); 2 = Barrio-Amorós and Ortíz (2015); 3 = Angarita-Sierra (2014); 4 = Pedroza-Banda et al. (2014); 5 = Trujillo (2015).

Country	State/department	Locality	Latitude	Longitude	Elev (m)	Source
Venezuela	Amazonas	Puerto Ayacucho	05.658314°	−067.605155°	65	1
	Apure	5 km SW Bruzual	08.022413°	−069.375284°	80	1
	Apure	Hato La Guanota, 4 km W San Fernando de Apure	07.878499°	−067.515509°	50	1
	Apure	6 km W San Fernado de Apure	07.878882°	−067.532976°	50	1
	Apure	Cinaruco river, 41 km NW Puerto Páez	06.410160°	−067.530089°	58	1
	Barinas	Barinas	08.632800°	−070.233104°	200	2
	Barinas	San Lorenzo, La Luz	08.333988°	−069.921837°	122	2
	Bolívar	Represa El Guri	07.766292°	−063.005544°	200	1
	Bolívar	16 km SE El Manteco	07.252686°	−062.425718°	240	1
	Guárico	Calabozo, Represa de Guárico	08.913677°	−067.430687°	100	1
	Guárico	Espino	08.557203°	−066.025056°	139	1
	Guárico	33.6 km N Corozo Pando	08.796467°	−067.586128°	79	1
	Guárico	15 km N Corozo Pando	08.639826°	−067.587906°	71	1
	Guárico	8 km N Corozo Pando	08.581404°	−067.586552°	70	1
	Guárico	8.7 km S Corozo Pando	08.428668°	−067.585618°	63	1
	Guárico	8.7 km N San Fernando de Apure	07.972784°	−067.466528°	51	1
	Guárico	El Sombrero	09.385825°	−067.061961°	166	1
Colombia	Arauca	Cravo Norte	06.300471°	−070.204199°	105	1
	Casanare	Trinidad, vereda El Banco de la Cañada, La Palmita farm	05.420681°	−071.600349°	165	3
	Casanare	Trinidad, vereda La Cañada, La Palmita farm	05.319833°	−071.347500°	146	4
	Casanare	Paz de Ariporo, Normandía village	05.672700°	−071.347500°	116	5
	Meta	Puerto Gaitán, Nueva Fundaciones village, 4.5 km E Manacacías River	04.215034°	−072.054604°	177	This work

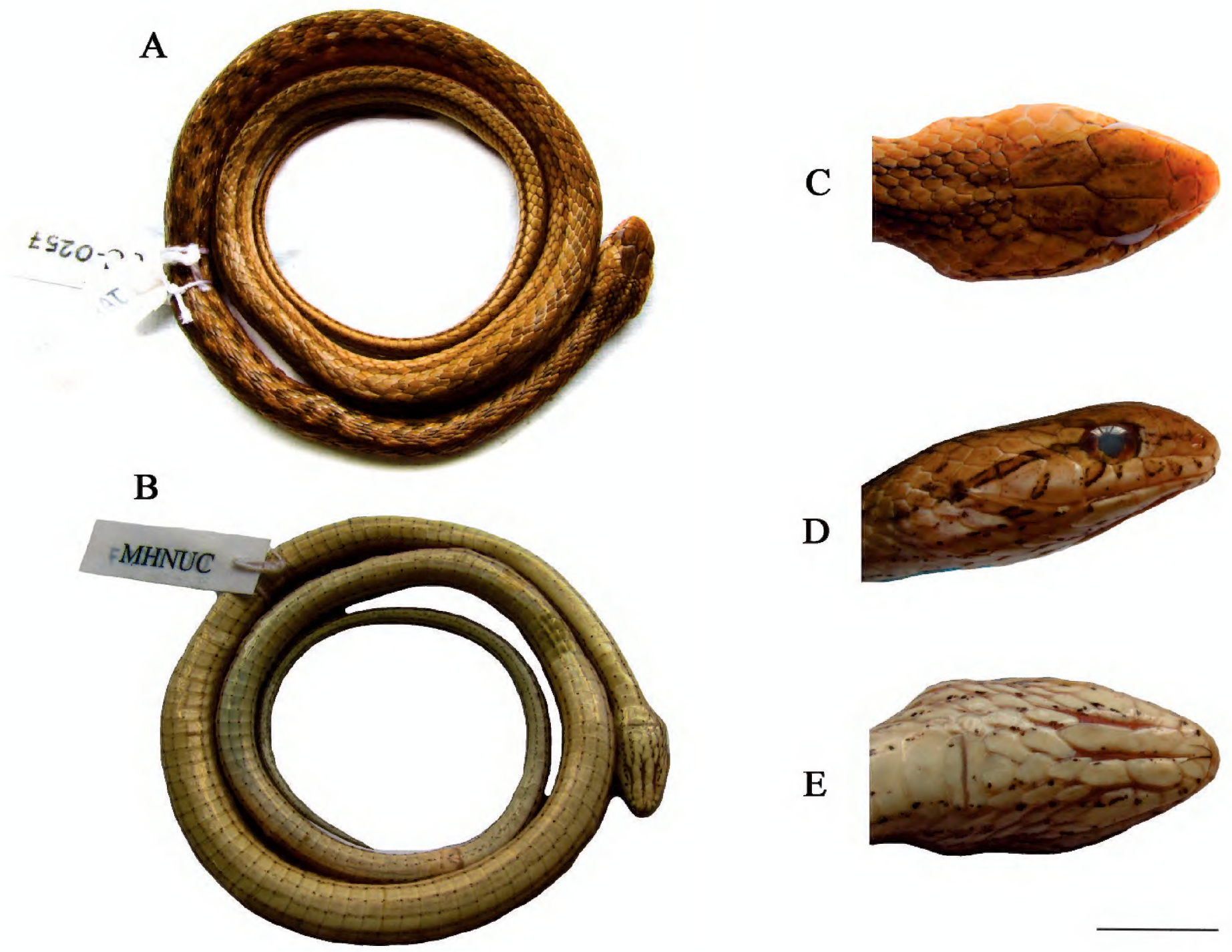

Figure 3. *Thamnodynastes dixoni* (MHN-UCa 0257; 380 mm SVL, 132 mm TL). **A.** Dorsal view. **B.** Ventral view. **C.** Dorsal head view. **D.** Lateral head view. **E.** Gular region view. Scale bar for C–E = 8 mm. Photographs by JARM.

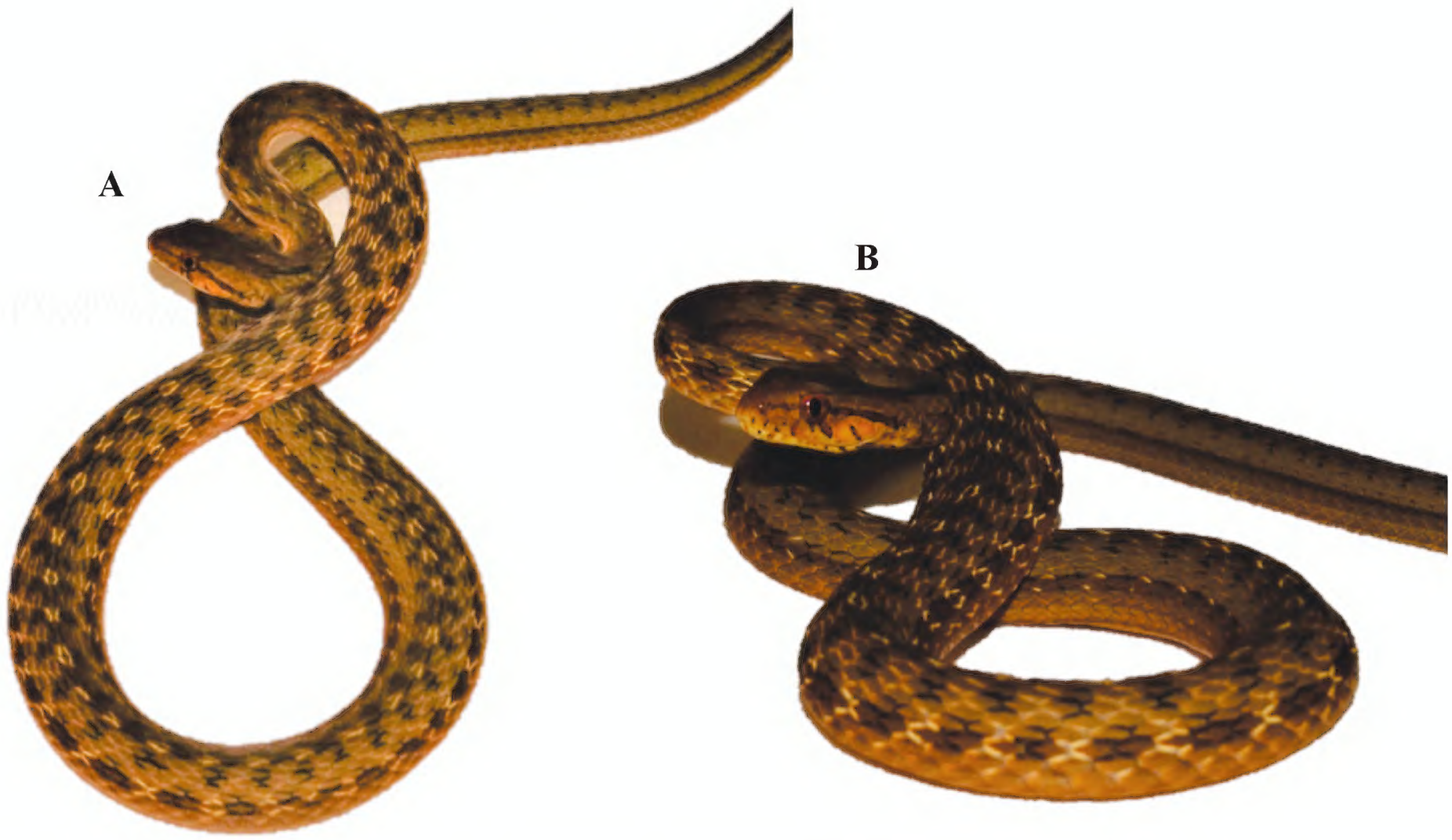

Figure 4. Corporal positions during the defensive behavior display of *Thamnodynastes dixoni*. **A.** Showing the S-shape dorsoventral body compression with lateral head enlargement. **B.** the body with an S-shape form and elevated approximately 45°. Photographs by JARM.

1758), *Oxyrhopus petolarius* (Linnaeus 1758), and *Ptychoglossus brevifrontalis* Boulenger 1912, are syntopic with *T. dixoni* at Nuevas Fundaciones village. According to Acosta-Galvis et al. (2010), the geographic range of *T. dixoni* is within the Llanos biogeographic subregion, which corresponds to the immense sedimentary flooded savannas (almost 600,000 km^2) between 20–500 m a.s.l., which was formed in the Tertiary and Quaternary. The Llanos is located between the Guiana Shield in the northeast, the Andes in the west, the Cordillera de la Costa in the north, and Amazonia in the south and southeast (Fig. 1). Open seasonal savannah is the dominant vegetation physiognomy, with gallery forests associated with the rivers and "morichales" (*Mauritia flexuosa* palms). Acosta-Galvis et al. (2010) reported 98 snake species in this region, and restricted to the Llanos sub-region six species: *Crotalus durissus pifanorum* Sadner-Montilla, 1980; *Crotalus vegrandis* Klauber, 1941; *Atractus punctiventris* Amaral, 1933; *Erythrolamprus pyburni* (Marckesich & Dixon, 1979); *Liotyphlops anops* (Cope, 1899); and *Micrurus medemi* Roze, 1967. There are no genera of snakes endemic to the Llanos. The local community of snake in the Llanos shows similar richness values (ca 14–20 species) for that observed in forested areas of the Caribbean and inter-Andean valleys of Colombia (Angarita-Sierra 2014; Angarita-M. et al. 2015; Vargas-Salinas and Aponte-Gutiérrez 2016), although the species composition is quite different. The general snake diversity in the Llanos region is lower when compared to Amazonia or Pacific ecoregions (Lynch et al. 2016).

Two species of *Thamnodynastes*, *T. pallidus* and *T. dixoni*, are known to occur in the Colombian Llanos. Barrio-Amoros and Ortíz (2015) stated that two specimens from Barinas, Venezuela were recorded in collections as *T. pallidus*. After a revision, these specimens were assigned to *T. dixoni* with no additional comments (Barrio-Amorós and Ortíz 2015). Although superficially similar, these two species differ in the number of dorsal scales rows (19 in *T. dixoni* vs 17 in *T. pallidus*) and the divided cloacal plate in *T. dixoni* (undivided in *T. pallidus*). To avoid confusing these two species, a careful review of *Thamnodynastes* species from eastern Colombia is necessary to determine possible areas of sympatry between *T. dixoni* and *T. pallidus*. The other two species of *Thamnodynastes* recorded in Colombia, *T. gambotensis* and *T. paraguanae*, are trans-Andean, distributed along the Caribbean coast of Colombia and Venezuela, including the Lake Maracaibo Basin (Bailey and Thomas 2007; Natera et al. 2015). Although morphologically similar, *T. dixoni* differs from *T. paraguanae* in the chin pigmentation, which is black and white in *T. paraguanae* and pale or well-striped in *T. dixoni* (Bailey and Thomas 2007). *Thamnodynastes gambotensis* is currently known to be restricted to the lower Magdalena river basin and the Caribbean coast in Colombia. Bailey and Thomas (2007) pointed out a form with a stout, spinous hemipenis similar to that of *T. gambotensis* from the eastern side of the Andes in eastern Colombia, which suggest that *T. gambotensis* occurs in the Llanos; however, they failed to mention vouchers to support their assumption. A search of online databases (Colección de Reptiles Instituto Alexander von Humboldt, IAvH 5143; https://www.gbif.org/occurrence/1801435781) found a cis-Andean record identified as *T. gambotensis* from Vichada near the Orinoco River, but it might represent a

misidentified specimen that was collected before the formal description of the species.

If *T. dixoni* is restricted to the Llanos, it is possible that the Guaviare River is the natural southern limit for this snake because this is the natural limit between Orinoquian and Amazonian ecoregions (Lasso et al. 2010). It is absolutely necessary to increase field efforts in these two ecoregions as well as to search for additional specimens housed in scientific collections to clarify this species' distribution across these contrasting ecoregions. Also, we recommend that research expeditions be made in the savannas of the Yarí River, which are a nucleus of anthropic Amazonian-Orinoquian savannas, with an area larger than 100 km^2, south from the Guaviare River. This area has been strongly transformed and has remained without biological studies due to the history of armed conflict in the 20th and 21st centuries (Osorno et al. 2019).

Finally, defensive behaviors in snakes are diverse and complex, with several of them supposedly associated with visually oriented predators (Greene 1988). Overall, defensive behavior is still poorly known for most species of Neotropical snake. Martins et al. (2008) found that Amazonian species of *Thamnodynastes* present defensive tactics that are similar to species of the genus *Xenodon* and *Sybinomorphus*. All these species show cryptic coloration and a repertoire of defensive behaviors including head triangulation, S-shape posture, and elevation of the anterior body, which are similar to those described for the genus *Bothrops* (Araújo and Martins 2006). *Thamnodynastes* defensive behaviors include ventral compression of the body with head enlargement, S-coil body shape, cloacal discharge, and striking (Natera et al. 2015; Magalhães et al. 2017; this paper). In particular, this behavior was described for *T. rutilus* in southeastern Brazil by Magalhães et al. (2017), who also recorded a strike with bite and cloacal discharge during manipulation of an animal. This suggests that *T. rutilus* might be able to adjust its defensive behavior accordingly to the threat. We observed that the defensive behaviors in *T. dixoni* are similar to those reported for *T. rutilus,* except that no cloacal discharge was observed. Additionally, *T. dixoni* only attacked after stimulated visually (at a distance 30 cm). This information is a contribution to the natural history of this poorly known species.

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Authors' Contributions

JARM collected and examined the specimen, wrote the draft, prepared the table, and drew Figures 2–4; HERC assisted JARM in the whole process especially in the preparation of the figures and first version of the manuscript; TBG assisted JARM with the identification of the species, in drawing Figure 1, and in writing the first version of the manuscript; all authors revised the manuscript.

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